REVIEWS

A Manual of California Vegetation. By John O. Sawyer and Todd Keeler-Wolf. 1995. California Native Plant Society, Sacramento, California. 471 pp.

This volume is arguably one of the most important ever to appear on the subject of California vegetation. It is significant because it is comprehensive—it attempts to classify and give a description of every known type of vegetation—and, perhaps even more because of its biopolitical implications—the authors are explicit that their aim its to make the manual the basis for setting vegetation-based priorities in the struggle to save California's diminishing natural ecosystems. It also carries special weight because it is the outgrowth of extended discussions of a large committee formed by the California Native Plant Society (CNPS) that included a broad spectrum of experts from universities, state and federal agencies, consulting firms, and private conservation organizations. It implicitly carries the imprimatur of the State of California because the second author is with the Department of Fish and Game, as were a number of committee members. A book with this lineage, this content, and these aspirations deserves careful review.

The nicely designed cover, with its striking photo, set a tone appropriate to the grandeur of the subject. This is further sustained by a collection of 32 plates with over 160 outstanding photos that may be the best comprehensive collection of color pictures illustrating California vegetation ever assembled in one book. Purchase of the book can almost be recommended solely on the basis this collection of photos.

The text consists of introductory and explanatory material (about 6% of the book), keys and descriptions of the individual vegetation types (series and others—about 73%), an extensive bibliography, an appendix describing the CNPS-approved sampling scheme, and indices of vegetation names, species, and a table that gives the equivalents between the Natural Diversity Data Base system developed by Robert Holland and the present system (hereafter Sawyer/Keeler-Wolf or SKW). The book is thus a "manual of vegetation" in the same sense that the keys and plant descriptions of a flora can be a "manual of the plants".

The scheme by which the diverse vegetation of this very large state is classified is said by the authors to be hierarchical, but they do not provide an overall description of the hierarchy. The keys work only for the central unit of their system, the "series". The series is not explicitly defined, but it is possible to deduce that it is a plant community that recurs at several to many sites with substantially the same species composition and structure and that is usually (but not always) characterized by the presence of one or a few defining species or genera that are usually (but not always) dominant. Rather surprisingly, no scale is specified for the series either as an individual stand occurrence or cumulatively for all stands, excepting the implicit requirement that a series be a repeating landscape unit. Thus, a single occurrence of a series in the landscape can be as small as a few meters across (duckweed series or quillwort series) or as large as many square kilometers (California annual grassland or creosote bush series).

The authors state clearly that their emphasis is on floristics and rarity. This leads to what some will surely consider a bias toward the vegetation equivalent of "splitting". Thus by SKW, most saltmarshes, ecosystems that have literally been the poster-communities for integrated function, will include several series (pickleweed series, cordgrass series). The overriding importance of floristics is further illustrated by the fact that the pickleweed series is said to occur both in salt marshes and in inland salt flats—only generic dominance, not habitat or ecological relations—matters. To many

ecologists, this approach will seem to have taken apart things that should be left together and to have lumped things that should be clearly distinguished.

The names of most series are composed of the common name of the single dominant species or the collection of names of the two or three dominants. Others series are named for genera (Quillwort series), and at least one by the life history of the dominants (California annual grass series). There are also "mixed series" where the dominance rule is relaxed to admit various dominance combinations of a small set of species (mixed conifer series). Each series is presented on a page or two in a systematic format that includes a brief description, geographical distribution (by a system very similar to, but not identical with, that used in the new *Jepson Manual*), a table that equates common and scientific names of species mentioned, a list of published quantitative descriptions of the series.

Many series descriptions also include lists of described "associations". This level of the hierarchical system, the only one other than series that is explicitly identified or discussed in the volume, is defined as a sub-unit of a series characterized by the presence or absence of particular species, usually in lower canopy strata (as in the incense cedar/twayblade association of the incense cedar series), but sometimes within the same stratum as the dominants (e.g., the incense cedar-Douglas fir association). There are many unanswered questions about the association. How, for example, in a hierarchical system, can an association be assigned to more than one series, as the authors state? Why is it that, in some instances, an association will have the same name as the series? The chamise-hoaryleaf ceanothus series has two named associations, one of which is the chamise-hoaryleaf ceanothus association. This seems odd. Is the same-name association a catch-all for everything that is not in the other associations? In another puzzling case, the dune lupine-goldenbush series has three associations, the heather goldenbush association (does this mean that no *Lupinus* is present?), the dune lupine association (no *Isocoma* or *Ericameria* is present?), and dune lupine-heather goldenbush association (everything else)? The many inexplicable instances in the implementation of the associations cry out for a fuller discussion in the introduction.

Dominance relations are the most fundamental aspect of the entire classification. It is therefore perplexing that dominance is only vaguely defined. A dominant is "an abundant species with high crown cover, especially in relation to other species in the stand". This leaves the reader in confusion as to whether dominance is an absolute or relative measure and exactly what "high" means. Study of various series suggests that relative cover is what is used in practice. Another key word in the SKW system is "important", which is applied to species that are not dominant, but are, well, important. As the lack of specific numbers to define these terms is too conspicuous an omission to be an error, one must assume that the authors preferred the flexibility afforded by nonquantitative definitions.

The flexibility theory is given weight by noting that, in some instances, quantitative criteria are provided in series descriptions—suggesting that more precise definitions of dominance are optional. Thus, for example, red shank series consists of stands having >60% red shank cover, but if red shank is 30 to 60% and another species within the same range, it is placed in a series defined by red shank and that other species, such as the red shank-chamise series. These quantitative guidelines do not eliminate all the problems. If stand A were 30% red shank and 55% chamise it would be classified as red shank-chamise. Referring to the chamise series, we learn that any stand with >60% chamise is in the chamise series, so that if stand B had 38% red shank and 62% chamise it would be the chamise series, even though the ratio of red shank to chamise and the cover of red shank would both be higher in B than in A. The system also opens the door to the peculiar situation in which there might be 30% red shank, 30% chamise, and up to 40% of some other species. Presumably this series would be called red shank-chamise, even though the third species was as abundant or more abundant than the two defining species.

The SKW system is unequivocally on the side of "describe what you see" and

rejects notions of speculating about "potential vegetation", as has been done in many vegetation mapping efforts. This solves one set of problems but creates others. In many circumstances, post-fire shrub vegetation is dominated by herbs and post-crown fire forest vegetation by shrubs. Surely the authors are not suggesting that such rapid and highly predictable successions are to be ignored? Yet no guidance is given on how to deal with them.

Because the series is at the heart of the SKW system, one might expect that the process by which series are defined would be explained in some detail. This is not the case. But the presence of the CNPS sampling protocol in an appendix and the comment in the text that the process of vegetation classification is "often long and detailed" implies that the authors have used or at least favor quantitative sampling and rigorous analysis for the description of series. This is underscored by the citations in the series descriptions of articles that present quantitative data. But the citations are highly diverse with respect to methodology, purpose, and comprehensiveness, and therefore it seems that the delineation of series cannot always have been based on "long and detailed" quantitative analysis. There is the suspicion that most series in the present volume were established subjectively and did not involve an analytical process analogous to that used by systematists to demonstrate that a new species is sufficiently distinct from existing species to deserve recognition.

The series is not, however, the only element of the system presented. They recognize three other categories similar to series: unique stands, habitats, and vernal pools. The "vernal pool" category is the most anomalous. The authors say that there is disagreement as to whether vernal pools should be treated from the vegetation or the ecosystem viewpoint, as though these were non-overlapping alternatives. They opt for the ecosystem view, which is odd, given that they have said earlier that floristics and rarity are the important factors. But what they call an ecosystem view is really more a biogeographical approach, since they divide the vernal pools into regional groups (e.g., Santa Rosa plateau vernal pools) and each group is described by the presence of particular plant species or genera. This will perhaps draw fire from the growing vernal pool invertebrate animal constituency, who argue that vernal pools with sparse or even no vascular plant cover are nonetheless vernal pools if they support characteristic animal assemblages. But more serious is the fact that providing vernal pools with their own unique category leaves it unclear where vernal pools fit, if anywhere, in the hierarchical scheme, and in series in particular. Using the series keys on southern California, vernal pools could lead to the spikerush series or the quillwort series for some pools or to totally inappropriate series for others. The keys don't direct the novice to "vernal pools", so anyone who uses the key at a small scale, which seems to be permitted in SKW, is in trouble unless they have a pretty good idea of what a vernal pool is independent of SKW. This raises the question: Why weren't vernal pools treated as series or perhaps in some cases as associations within the series in which they are found (annual grassland, chaparral, oak woodland)? It can't be because they are too small, since as we have seen, duckweed and quillwort patches can be series. It certainly isn't because the vegetation is not distinct, because there are many endemic species in vernal pools and the life histories and life forms are highly distinctive. The suspicion arises that this ambiguous treatment of vernal pools is explained by the recognition that if small habitats like vernal pools are to be included within the series system they either must be contained within other series (which might be politically dangerous) or that objective analysis will produce a proliferation of "series" along the lines of the chamise-red shank situation described above, only with many more potential dominants with much more restricted geographical ranges. If there is to be a set of series for pools, why not, for example, series for rock faces like the *Selaginella-Dudleya* series? The authors seem to be reluctant to promote that kind of fine-scale application of series, but are also reluctant to relegate a vegetation type of such conservation importance to a lower level of the hierarchy.

The purpose of the "habitat" designation is somewhat clearer. These are aggre-

gated vegetation types felt to deserve recognition but about which there is insufficient information to justify subdivision into series. Such problems seem to occur more frequently in the mountains, since six of the seven "habitats" are montane, and only one, "fen", is not specifically linked to mountains but probably will mostly be at higher elevations, except in the north coastal regions. The habitat designation raises questions about the seriousness of the commitment to a hierarchical approach. Habitats are a kind of interim higher unit. But if the SKW system had taken a top-down approach, there would be no need for interim treatment. Thus "montane meadow" could contain all future series corresponding to whatever criteria define this unit. It is not clear that this will be the case. But in contrast to the reluctance to define higher categories, SKW sees no problem with identifying lower units. They present quite long lists of associations contained within several of the habitat types. This raises a question: Is it possible in an objective hierarchical system to identify lower elements before the higher units are defined? Using the authors' own genus-species analogy for their hierarchy, it seems to be like identifying species without a concept of the genus.

"Unique stands" is the third ad-hoc grouping of vegetation types containing 24 vegetation units. The argument for the utility of this category is based on the authors' belief that recurrence of a particular species composition at multiple sites is fundamental to the definition of a series. They note that every stand of vegetation is unique, but evidently feel that some are more unique than others—thus this grab-bag of series wannabees that fail the "redundancy" test. Lack of redundancy seems to be particularly acute among California conifers (12 of the 24 unique stands) and of the rarer woody species in general (16 of 24). Rarity seems to be problematical because it reduces the number of sites at which a species is found. But beyond this, most of the unique stands are judged to be situations in which a single species pops up in vegetation that otherwise could be assigned to existing or future series. For example, SKW relegates Tecate cypress stands to "unique" status, but creates a series for Sargent cypress. A Tecate cypress stand looks pretty much like a Sargent cypress stand. So what is different? The only obvious difference is that Sargent cypress has a much broader range in the United States. Tecate cypress occurs in only two counties in the U.S. and has many fewer stands. Though one may suspect that range is a factor, that is not identified as the problem. The authors note that Tecate cypress "associates with local series rather than forming one". Thus Tecate cypress, which is locally dominant, flunks the series test by not being more discriminating in the species with which it associates. Evidently some unspecified degree of fidelity between a dominant and its co-occurring species is necessary and primary. We may speculate why Tecate cypress, which has probably been around for at least as long as Sargent cypress, seems to have been less able to form stable phyto-relationships than its sister taxon to the north. As with "vernal pools", unique stands seem to be an expedient indicating indecision or uncertainty on the part of the authors. They can't ignore these visually and floristically obvious phases of the vegetation, they don't feel they can make them a series, but neither are they willing to take the plunge and relegate them to a lower status of the hierarchy, presumably because that would violate the dominance principle and perhaps insult the local constituencies for these vegetation types.

The SKW scheme, like many other attempts at vegetation classification, places a heavy reliance on keys. It is assumed that the user has identified a "homogeneous" (not defined) area of vegetation (no scale specified) and either has actually sampled the area presumably following the CNPS guidelines or is experienced enough to estimate the various features needed visually. The reasonable assumption that the user has accurate identifications for all of the more abundant species in the highest canopy is also made. The first decision required by the key is whether the stand is dominated by herbs, shrubs, or trees. These are defined in the glossary in rather general terms. There is no fixed height definition for shrubs and trees. Shrubs are "short" when fully grown and tend to be multiple-stemmed, and trees are "tall" when fully grown

and tend to have one stem. The keys then subdivide the vegetation on the basis of many features, including growth form, taxonomic groupings, biogeographical groupings (e.g., "coastal scrub species"), and the degree of expression of dominance of the dominant species. Examples of choices are "Grasses dominant", "A *Cercocarpus* species not important", "Chaparrals where one species dominates".

It is clear that thought has gone into the keys, but they do not always function well. They differentiate the series primarily on the basis of presence, importance, and dominance of species, genera, growth forms (trees, shrubs, aquatics), life history types (evergreen), or, in a few cases, structural or biogeographical groups ("desert scrub species", "coastal scrub species"). Because of the lack of strict definitions of most of these terms, use of the keys will be most comfortable for those who are predisposed to fuzzy logic. Strictly binary thinkers will be frustrated trying to decide, for example, if species are "conspicuous" versus "not conspicuous".

Many ecologists will be vexed that a single series includes stands that occur on dramatically different substrates and in completely different geomorphological settings, and that successional stages are not recognized or dealt with in the system. To believers in continuous variation it is hard to overlook the fact that many, probably most, series grade into others and that boundaries are likely drawn arbitrarily.

In fairness to the authors, it must be noted that they do not present their system as a finished product. On the contrary, they see this publication as only the first iteration of an evolving program. They expect that other series will be defined, and though they don't say so, presumably they would not be averse to dropping or changing existing series or associations. The full hierarchy of vegetation will presumably also be presented sometime in the future, though this is not promised. But it is clear that they are assuming that change is going to be evolutionary, not revolutionary and that their newly hatched manual is a well adapted organism, and not a hopeful monster. But will SKW survive through the 21st century?

There are reasons to be skeptical. There is nothing in vegetation classification remotely as basic and compelling as the concept of genetic relatedness by virtue of inheritance in systematics. There is no "correct" answer for the question of how to deal with temporal and spatial variation in vegetation. It depends on the purpose. The vegetation classification that does the best job of distinguishing elements of the landscape worthy of preservation is unlikely to be the best system for describing the dynamic relations between different states of the vegetation, or to provide the units that are the best for mapping vegetation for management purposes. It is to be noted that the authors do not necessarily claim universality for their system, but they also fail to make a convincing case that their collection of series and associations constitutes the best or even an acceptably good system compared to some other for the primary purpose of informing conservation and management activities.

Most troubling is the underlying assumption of discontinuous variation. Bloody battles were fought in plant ecology from the 1930s through the 1960s over the fundamental nature of the plant community. Many of us thought that the Gleasonian individualistic hypothesis was the clear winner, and relegated typological thinking about vegetation to the dustbin of history. This smug confidence was premature, as SKW shows. The authors tip their hat toward Gleason in the introduction, but in the implementation the underlying paradigm clearly is one of discontinuous variation. The seem to say "California vegetation is complex, but it is patchwork with a relatively small number of kinds of patches. With enough study, we will be able to figure out how many kinds of patches there are". They don't think we have identified them all yet, but they are confident than in principal we will. They encourage the idea that "discovery" of new series and associations and publication of data describing them is an important task. This raises a frightening image of scholarly publications clogged with studies like "Seventeen new associations in the Mojave yucca series". There is, of course, a need for more and better data on the vegetation of California, but the decisions about where to spend the effort and how to design the studies should not guided by the needs of vegetation taxonomy.

It is useful to have a compendium of the different kinds of vegetation. SKW provides a valuable summary of the state of our knowledge and useful summary of one view of how many different kinds of vegetation we have. Its scholarship is impressive, but it is not the last word on how we should organize and understand the complexity of California vegetation. I can recommend buying the volume, but not the imposition of the system that it describes.

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Niebla and Vermilacinia (Ramalinaceae) from California and Baja California By Richard W. Spjut. Sida, Botanical Miscellany No. 14, Botanical Research Institute of Texas, Inc. 209 pp.

This monograph includes keys and descriptions for 71 North American species and one variety of *Niebla* and *Vermilicinia*, fruticose lichen genera, of which 53 species and the variety are new. These genera include highly polymorphic taxa that have been segregated from *Ramalina* sensu lato on the basis of vegetative anatomy and chemistry. *Niebla* sensu lato was proposed by Rundel and Bowler (1978) on the presence of medullary chondroid strands in most, abundant black pycnidia, and shared chemical features. *Vermilacinia* was segregated from *Niebla* sensu stricto by Spjut (1995), on the basis of distinctive secondary metabolites, and the lack of medullary chondroid strands and the reticulate surface ridging of *Niebla* sensu stricto. Included in *Vermilacinia* are species aggregates formerly called *Niebla combeoides* and *N. ceruchis*, while *Niebla* sensu stricto includes segregates from the former *N. homalea*. The many new species help to make sense of the highly polymorphic populations encountered in nature. About 2000 specimens were examined, mostly from the author's collections but also representing sizeable holdings from COLO, FH, US, and the C. Bratt private collection.

The North American distribution of the two genera is centered in the fog zone and Mediterranean California climate zone of the Pacific coast of California and Baja California, with some species extending as far north as San Juan Island, Washington, and a few others in South America, the Mediterranean, and Macaronesia. Twenty species of *Niebla* and 18 species of *Vermilacinia* are reported here for the United States. Those outside North America are not considered here.

Both morphologically based and chemically based keys are provided. The morphological key, while having some ambivalent dichotomies, is generally workable after some effort in learning how specific terms are used by the author. Detailed morphological descriptions are given for each species, as well as chemistry, distributions, and lists of representative specimens. Some species pairs apparently differ only chemically. Terminology is complex but explained in detail in a section of the text as well as in a glossary. A few terms still appear ambiguous: "glossy" versus "glabrous, creamy" surface, for example.

It is a pleasure to encounter a lichen monograph that contains numerous illustrations of the "plants", apart from those showing their internal structure and chemistry. There are 66 color photographs, most showing close-up views of individual organisms, but also several showing habitat. One or more excellent-quality black and white photographs with scale is provided for each species. Drawings included in the keys, however, are variable in quality. Maps show floristic provinces and collecting locations for each species. Many endemic taxa are included; endemics are rather unusual among lichens.

Richard Spjut has produced a workable treatise on two difficult genera of lichens, which have seemed intimidatingly polymorphic. He has brought together a useful compilation of the current status of information about *Niebla* and *Vermilicinia*, as well as on the climatic types, vegetation zones, and phytogeography of the regions